Systematic Position and Relationships of the Percesocine Fishes[1]

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THE FISH FAMILIES Sphyraenidae, Mugilidae, and Atherinidae have been assigned to the percesocine fishes by all authors, and many would include only these (e.g., Berg, 1940: 368). Others have expanded the group in various ways (e.g., Boulenger, 1904: 636). Most commonly, however, such expansion has extended only to the family Polynemidae (e.g., Regan, 1912: 846) or, in recent years, to the polynemid and phallostethoid fishes (e.g., Myers, 1935: 6).

Generally, the percesocine fish groups have been placed at the front of or just ahead of the order Perciformes. The major question in this regard is whether they represent derivatives of a percoid or of a pre-percoid stock.

In the present investigation some attempt has been made to determine the interrelationships and systematic position of the Sphyraenidae, Mugilidae, Atherinidae, and Polynemidae. For this purpose Hawaiian specimens of *Sphyraena barracuda* (Sphyraenidae), *Mugil cephalus* (Mugilidae), *Pranesus insularum* (Atherinidae), and *Polydactylus sexfilis* (Polynemidae) have been stained with alizarin and dissected. To base conclusions regarding families on such limited material is obviously a treacherous undertaking. However, the Sphyraenidae, Mugilidae, and Polynemidae are rather closely-knit families and it is assumed that, for these, any species is fairly representative. For the Atherinidae the situation is quite different. Indeed, Jordan (1923: 177) split the Atherinidae as usually conceived into four separate families. It is therefore highly possible that the structures described for *Pranesus* would be quite different in atherinid genera such as *Craterocephalus* or *Melanotaenia.*

No phallostethoid fishes have been available. However, a considerable literature exists on the anatomy of these forms (Regan, 1916; Bailey, 1936; Villadolid and Manacop, 1934; Aurich, 1937; Hubbs, 1944). On the basis of this, some discussion of phallostethoid relationships has been included.

The conclusions reached here are not new, but it is hoped that the material presented will help to establish them on a somewhat sounder basis than heretofore.

PELVIC STRUCTURE

As a group, the four families Polynemidae, Mugilidae, Sphyraenidae, and Atherinidae have been separated from the typical percoid fishes almost solely on the basis of the subabdominal pelvic position (Regan, 1929). Some attempt to evaluate the systematic significance of this character seems in order.

Regarding the Atherinidae, Boulenger (1904: 639) stated: "Pelvic bones connected with the clavicular [cleithral] symphysis by a ligament." Gregory (1933: 262) wrote: ". . . at least in *Sphyraena ideastes,* a long ligament runs from the pelvis to the cleithral symphysis (as I noted in dissecting a fresh specimen)." Dollo (1905) used Boulenger's statement as a basis for the hypothesis that the abdominal or subabdominal position of the pelvic fins in various families including the four under consideration was a result of secondary regression from the percoid-type pelvic location.

Efforts by the present author to find a ligament between the pelvic girdle and the cleithral symphysis in *Polydactylus, Mugil, Sphyraena,* and *Pranesus* have been unsuccessful. There are ligaments running forward from the bases of the pelvic rays to the pelvic musculature. There are also ligaments running back from the cleithral symphysis to the musculature of the body (Fig. 1*a*). These two sets of ligaments do not meet, however, in any of the four species examined. (The ligament that runs between the anteroventral tip of the pelvic girdle and the lower portion of the pectoral girdle in *Holocentrus* (Fig. 1*a*) seems to be completely lacking in all percesocine fishes investigated.)

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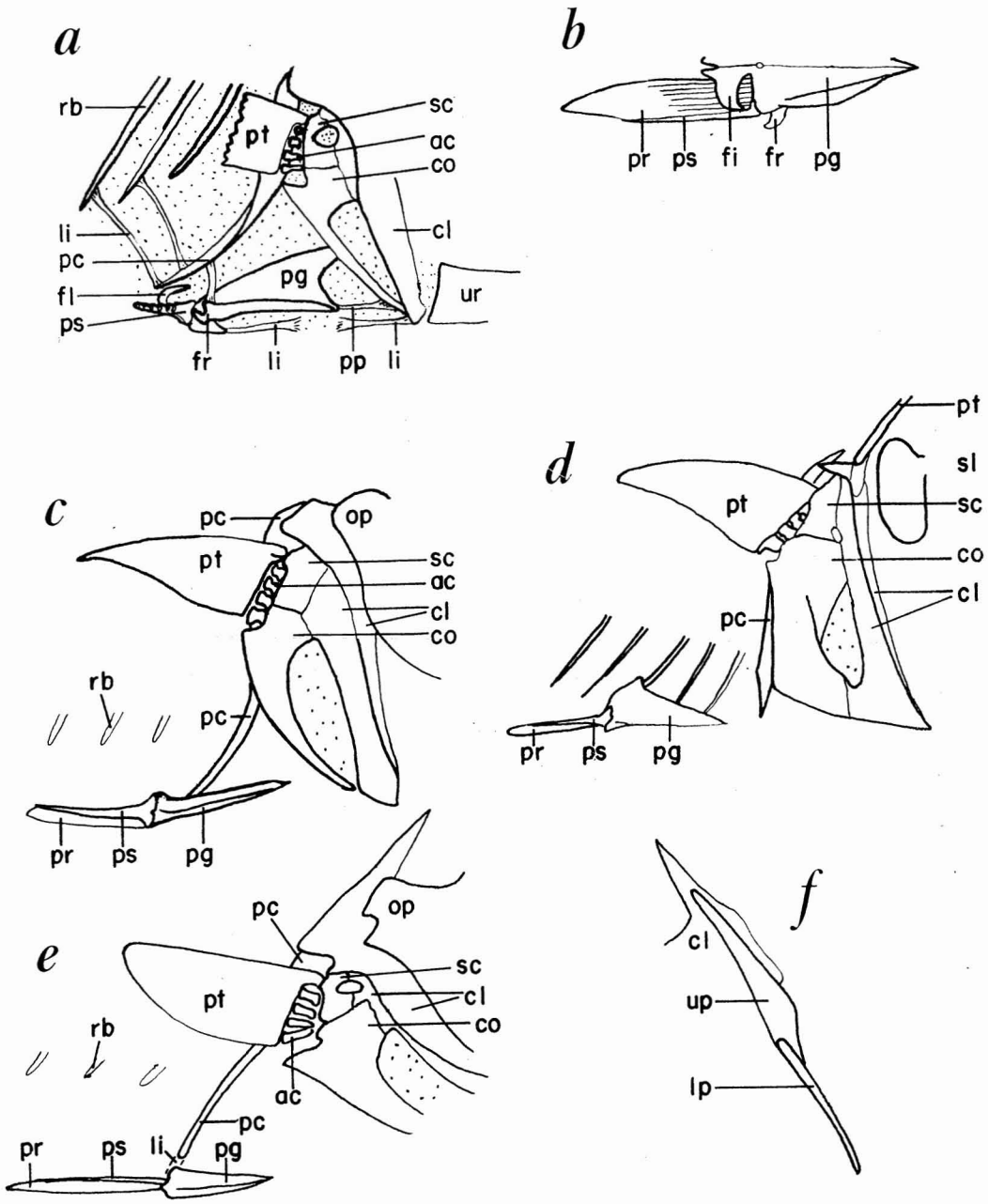

FIG. 1. Pelvic-pectoral relationships, semidiagrammatic. *a, b, Holocentrus lacteoguttatus; c, Mugil cephalus; d, Pranesus insularum; e, f, Sphyraena barracuda. a, c, d, e,* Right side in lateral view; *b,* right half of pelvic girdle from above; *f,* right postcleithral strut from inside. *ac,* Actinost; *cl,* cleithrum; *co,* coracoid; *fl,* flange that abuts against tip of postcleithrum; *fr,* flange for attachment of ligament from postcleithrum; *li,* ligament; *lp,* lower postcleithrum; *pc,* postcleithrum; *pg,* pelvic girdle; *pp,* pelvic-pectoral ligament; *pr,* pelvic rays; *ps,* pelvic spine; *pt,* post-temporal; *rb,* rib; *sc,* scapula; *sl,* supracleithrum; *up,* upper postcleithrum; *ur,* urohyal.

Boulenger (1904: 641, and fig. 391) also points out that in the Polynemidae the pelvic bones are suspended from the postclavicles, i.e., postcleithra. Among the four families under consideration postcleithral struts supporting the pelvic girdle on either side are found in *Polydactylus, Mugil* (Fig. 1*c*), and *Sphyraena* (Figs. 1*e*, *f*) but not in *Pranesus*. In *Pranesus* (Fig. 1*d*) the pelvic girdle may be supported to some extent by the tips of the first three pairs of ribs (i.e., the pleural ribs of vertebrae three, four, and five), but of the three only the third has any strong ligamentous attachment between its tip and the pelvic girdle.

No such postcleithral or rib abutment against the pelvic girdle was found in any of the perciform genera examined: *Epinephelus, Apogon, Priacanthus, Caranx, Mulloidichthys, Chaetodon, Acanthurus,* and *Eleotris*. In the deep-bodied genera *Priacanthus, Caranx, Chaetodon,* and *Acanthurus,* the postcleithra are long and strong but pass down behind the pectoral girdle. This last type of postcleithrum occurs in the zeiform genus *Antigonia,* which has the anterior portion of the pelvic girdle attached to the cleithral symphysis as in the percoids. Judging from an X-ray photograph of the lampridiform genus *Metavelifer,* its pelvic girdle has the same relationships as in the percoids and *Antigonia.*

A postcleithral abutment against the pelvic girdle is not unique, however, to the Polynemidae, Mugilidae, and Sphyraenidae. It occurs again (among the fishes examined) in the berycoid genera *Holocentrus* (Fig. 1*a*) and *Myripristis*. However, in the polynemids, mugilids, and sphyraenids the postcleithra are attached directly or indirectly to the outer rim of the pelvic girdle ahead of the fin articulation, whereas in *Holocentrus* and *Myripristis* the postcleithral abutment is against an expanded flange behind the pelvic ray articulation (Fig. 1*b*). Furthermore, the front of the pelvic girdle of *Holocentrus* is firmly wedged into the musculature between the lower ends of the pectoral girdle and attached to it by both muscles and a ligament (Fig. 1*a*), whereas the pelvic girdle of the percesocine fishes is not. In view of the above and of Regan's statement (1912: 839) that in the berycoid *Trachichthys* the pelvics are directly attached to the pectoral girdle, it would appear that the holocentrids could provide better examples than the percesocine fishes for Dollo's hypothesis of a secondary backward movement of the pelvics.

A rather casual search of the literature has shown that a postcleithral support for the pelvics also occurs in the syngnathiform genus *Centriscus* (Jungersen, 1908: 88, and pl. 2, fig. 2; see also his footnote 14 on p. 105). However, in the other syngnathiform genera studied by the same author (Jungersen, 1908, 1910) there is no attachment of any sort between the pelvic and pectoral girdles.

In view of the above discussion it seems somewhat unsatisfactory, or at least questionable, to postulate a secondarily abdominal position for the pelvic fins of the percesocine fishes. A different and, to the present writer, preferable explanation is that the support provided for the pelvic fins by the postcleithra represents a level of structural stabilization in the general trend toward forward movement of the pelvics in teleostean evolution. To accept such an explanation, as will be done here, does not imply (1) that the various groups with a postcleithrum-pelvis abutment has developed only once, (2) that the pelvic fins have never moved back in the course of teleostean evolution, or (3) that the development of the postcleithral pelvic support has provided an especially successful or stable stage of structural organization.

Only one working hypothesis with regard to the above thesis will be discussed here. So long as the pelvic fins have no pungent defensive spines, attachment to a pelvic girdle that lies free in the body wall would seem to be a satisfactory arrangement. When, however, the pelvics develop pungent spines, a more secure emplacement of the pelvic girdle would appear advantageous. There is some evidence to bear out this hypothesis. Among the fishes investigated, *Polydactylus* and *Mugil* (Fig. 1*c*) have stiff, sharp pelvic spines and firm postcleithral abutments against the girdles. In *Sphyraena* (Fig. 1*e*) and *Pranesus* (Fig. 1*d*) the outer pelvic rays, by contrast, are relatively slender and somewhat flexible. In *Sphyraena* the postcleithrum does not abut directly against the pelvic girdle but is merely attached to the girdle by ligamentous tissue; in *Pranesus* the girdle is held in place, as already noted, merely by the tips of abdominal ribs.

There appear to be only three ways in which

fishes have attained a firm emplacement for pungent pelvic spines. One is the extension of the pelvic girdle over the body wall as a large dermal plate, as in *Gasterosteus*. The second is the abutment against a postcleithral strut. The third is direct attachment anteriorly to the cleithral symphysis. Presumably, once a fish with pungent pelvic spines has developed one of the above three types of pelvic support, it will retain it. For such fishes, any of the three types would seem to provide a level of structural stabilization in evolution. However, for those fishes without pungent pelvic spines none of the three types of girdle support would seem to be of any great value, and it is presumably in such fishes that changes in pelvic position have evolved.

POLYNEMIDAE, MUGILIDAE, SPHYRAENIDAE, AND ATHERINIDAE

The polynemids have usually been separated from the mugilids, sphyraenids, and atherinids on the basis of pectoral peculiarities (Regan, 1929; Berg, 1940). The last three families have long been placed together. Nevertheless they differ widely from one another. Starks (1899: 1), in a report on the osteology of several members of these families, remarked:

In examining the crania of these species, attention is attracted at once to the fact that in all of them the epiotics are developed into long, thin processes which divide into more or less bristle-like filaments.

There is little else in purely internal characters whereby to differentiate these families as a group from other Acanthopteri. In order to so differentiate them we must turn to the well-known external characters—a spinous dorsal in conjunction with the abdominal ventral fins, high pectoral fins, and unarmed opercles.

With regard to the characters listed, *Pranesus* has no epiotic processes, and *Sphyraena* has a moderately low pectoral and a more or less "armed" opercle (Fig. 1*e*). Inasmuch as no new distinguishing characters held in common by sphyraenids, mugilids, and atherinids seem to have been discovered since Starks wrote, the three families form a group for which no very clear-cut definition is available.

As to the interrelationships of the three families, Starks (1899: 1) stated:

If, however, we eliminate the Sphyraenidae (which, on account of its fanglike teeth, set in deep sockets, its separate superior pharyngeals of third and fourth branchial arches, its lack of parapophyses on anterior vertebrae, and other characters, we may well be justified in doing) and place it in a separate superfamily coordinate with that in which we place the Mugilidae and Atherinidae, we shall then have a more compact group, notwithstanding the great difference in number of veterbrae in the two families of which it is composed.

Of the sphyraenid peculiarities mentioned, the teeth are certainly a specialization related to the predaceous habits of the barracudas. However, Jordan and Hubbs (1919: 6, footnote 3) have pointed out that some of the larger atherinids have strong teeth in shallow sockets, thus approaching the sphyraenids in this feature. In most other characters, however, *Sphyraena* "seems to be a much more generalized form than other members of the Percesoces" (Starks, 1902: 622, footnote 1).

With regard to the relationships of the Polynemidae, Regan (1912: 846, 847) included them with the other three families in an order Percesoces with the statement:

Contrary to what has usually been supposed, the Polynemidae are more closely related to the Sphyraenidae than to the Mugilidae, as is shown in the subjoined synopsis of the families.

I. A lateral line; pectoral fins placed low. Cranial crests well developed (Polynemidae) or vestigial (Sphyraenidae). Exoccipitals meeting above basioccipital; alisphenoids meeting. Supra-clavicle moderate. Parapophyses, when developed, downwardly directed. Twenty-four vertebrae.
   Pectoral fin normal; parapophyses on posterior praecaudals only.....1. Sphyraenidae
   Pectoral fin of two parts, the lower of detached filamentous rays; pterygials represented by a plate attached to the edge of the scapula and coracoid; parapophyses from the third vertebra .....2. Polynemidae

II. Lateral line incomplete or absent; pectoral fins usually placed high. No cranial crests; exoccipitals separate; alisphenoids separate. Supraclavicle small. Parapophyses well developed, anteriorly nearly horizontal.

24 to 26 vertebrae.....3. Mugilidae
32 to 60 vertebrae.....4. Atherinidae

It seems unnecessary to discuss the above arrangement since in his later work Regan (1929) returned to the more usual system of recognizing the Polynemidae on the one hand and the Sphyraenidae, Mugilidae, and Atherinidae on the other as two separate suborders of the order Percomorphi (= Perciformes).

In the following paragraphs certain hitherto neglected structural systems will be described and others will be discussed. Suffice it to say in advance that in most of these the Atherinidae (at least as represented by *Pranesus*) appears to have diverged farther from the basal percesocine stock than the Polynemidae, Sphyraenidae, or Mugilidae.

BODY AND HEAD SHAPE: *Polydactylus,* like most fishes, has a rather high back and head. *Sphyraena, Mugil,* and *Pranesus* and most members of their families are, by contrast, flat backed and flat headed. Several morphological characters, in all of which *Polydactylus* is the more generalized, would seem to be associated with this difference.

Polydactylus also differs from the others in the decidedly inferior mouth. This has led to some osteological peculiarities in the snout region. However, these features will not be stressed, since other genera of polynemids have a far less inferior mouth than *Polydactylus.*

SKULL: The crania of sphyraenids, mugilids, and atherinids have been dealt with at some length by Starks (1899); and Gregory (1933) gives a rather unsatisfactory figure of the head skeleton of *Polydactylus.* The only aspect of the crania that will be discussed here is one presumably associated with differences in the body shape previously noted.

In *Polydactylus* the skull has the usual percoid-type supraoccipital and frontal-parietal crests. These provide extensive surfaces for the attachment of the body muscles, which run forward over the rear of the skull. In the flat-headed *Sphyraena, Mugil,* and *Pranesus* the supraoccipital does not rise above the surface of the skull and the frontal-parietal crests are at best represented by vestigial ridges (Regan, 1912: 846). The body musculature does not extend forward over the rear of the skull, and its total area of attachment is provided by the rear face of the skull and such bony areas as may extend back from it. Presumably it is the need for areas of muscular attachment which has led to the development of backwardly projecting bony, brush-like extensions from the head in large species of mugilids and atherinids, but most notably in *Sphyraena* (Starks, 1899: 1, pls. 1, 2).

JAW STRUCTURE AND TEETH: The jaw structure and teeth of the fishes under consideration vary considerably, presumably in association with differences in feeding habits. The large, socketed teeth of *Sphyraena* have already been noted.

Eaton (1935) drew attention to the similarity in jaw structure between *Fundulus* and the atherinids. Gosline (1961) subsequently pointed out that the jaws of *Fundulus* and atherinids have a very different structural organization, that of the atherinids, mugilids, and sphyraenids being derivable from a typically percoid type. Of the four fishes dissected, *Sphyraena* is the only one that retains a supramaxillary.

SUPERFICIAL BONES OF SNOUT AND CHEEK REGION: Probably in relation to the inferior position of the mouth, the whole anteroventral end of the snout of *Polydactylus sexfilis* appears to have been rolled back under the orbit. Thus the front of the lacrimal does not even reach the anterior rim of the orbit (Fig. 2*b*), whereas the nasal bone not only forms a cup over the front of the nasal capsule but has a flat flange extending downward from the lower rim of the cup. The anterior end of the supraorbital canal is carried on the outer surface of the cup to a point somewhat below the olfactory organs. (In *Polydactylus sexfilis* both the nasal bone and the anterior end of the lacrimal are deeply embedded in adipose tissue, which is in turn covered by scales.) The lacrimal, which bears the anterior end of the infraorbital canal in the fishes under consideration, extends back along the whole lower border of the orbit in *Polydactylus* (Fig. 2*b*), and rather broadly overlaps all but the posterior portion of the maxillary when the mouth is closed. The anterior end of the lacrimal fits over and articulates with the tip of the lateral ethmoid. The lacrimal is, however, a very thin bone without serrated edges. Behind it are five circumorbitals that carry the infraorbital canal to its junction with the supraorbital canal. The lowermost of the five has a rather regular, tri-

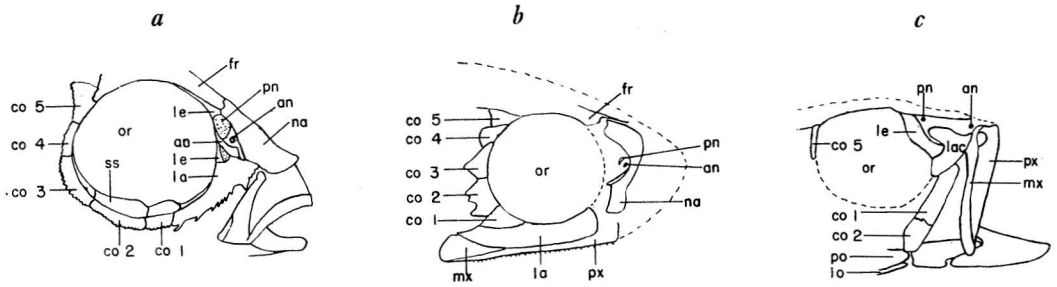

FIG. 2. Bones of the sides of the head in *a, Holocentrus lacteoguttatus, b, Polydactylus sexfilis,* and *c, Pranesus insularum,* all semidiagrammatic. *an,* Anterior nostril; *ao,* antorbital; *co 1–5,* circumorbital bones (not including the lacrimal or antorbital); *fr,* frontal; *io,* interopercle; *la,* lacrimal; *le,* lateral ethmoid; *mx,* maxillary; *na,* nasal; *or,* orbit; *pn,* posterior nostril; *po,* preopercle; *px,* premaxillary; *ss,* subocular shelf.

angular shape, but the upper three have irregular, flap-like posterior extensions. A subocular shelf (not shown in Fig. 2*b*) is represented in *Polydactylus* by a small strut from the second circumorbital extending in along the posteroventral border of the orbit.

The circumorbital bones of *Polydactylus* differ in a number of ways from those of the other three species examined. Among the latter, *Sphyraena* is the only genus with a complete circumorbital series—lacrimal plus five circumorbitals—and the only one in which the infraorbital sensory canal extends continuously from the lacrimal back to its junction with the supraorbital canal. In *Mugil* the lacrimal is completely separated from the small ossicles around the rear of the orbit that make up the rest of the series. In *Pranesus* (Fig. 2*c*) the lacrimal and first two circumorbital bones are widely separated from the other small circumorbitals along the rear border of the orbit. In none of these three percesocine fishes is there any sign of a subocular shelf.

Probably in relation to the inferior mouth of *Polydactylus,* it is the anterior (rather than the posterior) end of the lacrimal that wedges against the lateral ethmoid. In the other three genera investigated, the lacrimal is held in position in different ways. In *Mugil* and *Sphyraena* the rear of the lacrimal is wedged under the lateral ethmoid and the front under the nasal. In *Sphyraena,* the lacrimal is a long triangular bone; in *Mugil cephalus* it is short and stout, with a serrated posteroventral border. The anterior circumorbital bone arrangements of *Pranesus* are most unusual. The lacrimal forms a plate over the lateral ethmoid; extending obliquely down and back from the lacrimal are the two anterior circumorbitals. The posterior end of the second overlaps and has a firm ligamentous attachment to the anteriormost point on the preopercle. Here, as in the scorpaeniform and gasterosteiform fishes, there is a suborbital stay, but in *Pranesus* this runs down to the *front* of the preopercle. The peculiar axis of this suborbital stay is doubtless associated with the obliquity of the mouth in *Pranesus.* (To what extent it occurs in other atherinids I have not the material to determine.)

The nasal bones of *Sphyraena, Mugil,* and *Pranesus* do not form a cup around the front of the nasal capsule as in *Polydactylus,* but extend for the most part straight forward along the superolateral border of the snout region.

NASAL ORGAN AND NOSTRILS: The nasal organ of *Polydactylus sexfilis* is seated deep in the adipose tissue of the snout directly ahead of the middle of the eye. The two nostrils are close together, the anterior a little lower than the posterior (Fig. 2*b*). The front nostril is a roundish hole with a flap on its rear border that partially covers the posterior nostril, which is somewhat elongated vertically. Both nostrils extend in through the adipose tissue to the nasal sac. The nasal rosette has a central rachis that runs downward and forward. In a 110 mm specimen there are about a dozen lamellae extending out from either side of the rachis.

In the other genera the two nostrils of each side are high on the head and well separated

from one another (Fig. 2*c*). The three available genera differ widely from one another, however, in the structure of the nasal rosette. In *Mugil cephalus* it has an elongate rachis with numerous well-developed lamellae extending out to either side; in *Sphyraena* the nasal rosette is reduced, with a few rudimentary lamellae on either side; and in *Pranesus* the nasal organ seems to be represented by four longitudinal flaps that lie beside one another.

OPERCULAR BONES: The opercular bones of *Polydactylus* are sufficiently shown in Gregory's figure (1933: 268, fig. 144). Though the preopercle of *Polydactylus,* unlike that of the percesocine fishes (sensu stricto), is serrate, that of the related *Pentanemus* is said to be entire. There seem to be no other major differences between the opercular bones of *Polydactylus* and those of the percesocine fishes.

PHARYNGEAL TEETH: According to Starks (1901: 2, 3), in the Atherinidae and Mugilidae the third and fourth upper pharyngeals are anchylosed; in the Sphyraenidae they are not. *Polydactylus sexfilis* is like *Sphyraena* in this respect.

PECTORAL GIRDLE: According to Starks (1899: 2, 3) the lower limb of the post-temporal is attached to the opisthotic [= intercalar] by a dentate suture in the Mugilidae, but not in the Sphyraenidae and Atherinidae. Stated in slightly different terms, the post-temporal is rigidly attached to the skull in the Mugilidae (by both the upper and lower limb), but is movably attached in the Atherinidae, Sphyraenidae, and also in the Polynemidae. The fusion of the post-temporal to the skull in *Mugil* is perhaps related to the development of the peculiar pharyngial apparatus that occupies the space below and between the post-temporals in that genus.

The divided pectoral fin and associated girdle features (Starks, 1926: 194, fig. 18) of polynemids are unique, and form the usual basis for separating the Polynemidae from the other three families. Among the latter, Starks (1926: 193) notes that in the atherinid *Atherinopsis* the uppermost actinost may become completely fused to the scapula. (The reduction in the number of actinosts ascribed to the phallostethids by Bailey (1936) may have occurred in the same fashion.)

FIN STRUCTURE AND FIN SUPPORTS: Hubbs (1944) has provided a detailed comparison between the fin structure of the phallostethids, atherinids, mugilids, sphyraenids, and polynemids, pointing out the rather striking resemblances between the fins of the five groups. Hollister (1937) has described the caudal skeleton of certain sphyraenids, mugilids, and atherinids. Gosline (in press) has suggested that the caudal skeletons of these families plus the polynemids could be interpreted as increasing structural specialization away from the basic percoid type in the series *Polydactylus-Sphyraena-Mugil-Pranesus.* Bridge (1895) has described the dorsal and anal fins and fin supports in *Sphyraena* and *Mugil.* He points out that the endoskeletal supports of certain of the soft dorsal and anal rays of *Sphyraena* are trisegmental, a characteristic feature of lower teleostean fishes found for the last time in a few basal percoids. The present account deals only with the relationship between the endoskeletal supports of the spinous dorsal and the vertebral column.

DORSAL ENDOSKELETAL STRUCTURES: In all four fishes investigated there are two sorts of dorsal endoskeletal structures: those that support dorsal fin rays and those that do not. Structurally the two types seem to grade into one another. Nevertheless, for purposes of description the endoskeletal elements supporting fin rays will be called pterygiophores and those that do not supraneurals, following Eaton's (1945) terminology.

In *Polydactylus* (Fig. 3*a*) there are three supraneurals above the first three vertebrae. Following this there are seven pterygiophores (bearing eight spines), which hold a one-to-one relationship with the vertebrae below them. Behind the last of these there is a gap one vertebra in width, followed by the first pterygiophore of the second dorsal. (The anteriormost ray in this fin is a spine.) This arrangement of endoskeletal supports closely parallels that of the lower percoid fishes (Katayama, 1959: 148–149, figs. 24–28). The one peculiarity seems to be the absence of a supraneural between the two dorsal fins; in this feature *Polydactylus* parallels *Mulloidichthys* (Mullidae) but not *Apogon* among percoids with separate dorsals. In *Mugil* (Fig. 3*c*), *Sphyraena* (Fig. 3*d*) and *Pranesus* (Fig. 3*b*) there are supraneurals between the two dorsal fins, but those of *Sphyraena* are rudimentary.

In *Sphyraena, Mugil,* and *Pranesus* there has been a condensation of the spinous dorsal base resulting in two or more pterygiophores over each vertebra. In *Mugil* (Fig. 3*c*) the pterygiophores still interdigitate between the tips of the neural spines, but in *Pranesus* (Fig. 3*b*) the pterygiophores form a discontinuous plate of bone that lies entirely above the neural spines. *Sphyraena* (Fig. 3*d*) is intermediate between *Mugil* and *Pranesus* in this respect.

With regard to position, the first pterygiophore of *Polydactylus* lies over the 3rd neural spine, that of *Sphyraena* over the 4th, of *Mugil* over the 7th and 8th, and of *Pranesus* over the 15–18th.

Mugil and *Sphyraena* retain the three supraneurals ahead of the spinous dorsal, but in *Pranesus* they are gone.

VERTEBRAL COLUMN AND RIBS: In the specimens of *Polydactylus, Mugil,* and *Sphyraena* dissected the total number of vertebrae is 24. Jordan and Hubbs (1919: 6) give a vertebral range of 24–26 for the Mugilidae. In the Atherinidae (Jordan and Hubbs, 1919: 7) the vertebral count is always more than 30.

In *Polydactylus* and *Sphyraena* all of the neural spines taper dorsally to a point, as is usual in fishes. In *Mugil* and *Pranesus,* however, some of the anterior neural spines are flattened and blade-like (Fig. 3*c*), as was noted for the Mugilidae and Atherinidae by Starks (1899: 2).

The articulation between the skull and the first vertebra is quite different in *Polydactylus* and *Sphyraena* on the one hand and in *Mugil* and *Pranesus* on the other. In the skull itself this difference is reflected in the separation of the exoccipitals noted by Regan (1912: 846). So far as the first vertebra is concerned, its neural arch and centrum are separately movable in *Polydactylus* (Fig. 3*a*) and *Sphyraena* (Fig. 3*d*), fused in *Mugil* and *Pranesus.*

Starks also used the absence of parapophyses on the anterior vertebrae of *Sphyraena* as a basis of differentiating this genus from the atherinids and mugilids. However, *Sphyraena* does have parapophyses on vertebrae 5 through 9 (Fig. 3*d*), though these are not nearly so well developed as in the other fishes examined.

One final vertebral feature may be noted because of its bearing on phallostethid structures. In *Polydactylus, Sphyraena, Mugil,* and *Pranesus* the first pleural rib is that on the third vertebra, with which it articulates firmly. This is the typical condition for the basal percoid fishes (Boulenger, 1895: 2–5, 114–115).

PHALLOSTETHOID FISHES

Since their discovery in 1913 the phallostethoid fishes have received a good deal of attention. Much of this has been directed toward elucidating the structure of the unique clasping organs of the males. With regard to systematic position Regan (1913, 1916) originally included the phallostethoids among the cyprinodont fishes. Myers (1928, 1935) subsequently placed them among the percesocine fishes nearest the Atherinidae. Finally, Berg (1940: 465) recognized the phallostethoids as a separate order.

Judging from the literature, the phallostethoids cannot possibly be placed among the cyprinodont fishes. For one thing some phallostethoids have a small, separate spinous dorsal. For another they have the typical berycoid-percesocine-percoid type of upper jaw protrusion rather than the peculiar type that seems to have been developed within the cyprinodonts (Gosline, 1961). The conclusion seems inescapable that the phallostethoids have been derived from some percesocine or percoid stock.

So far as pelvic structure is concerned, the pelvic fins are either absent or rudimentary. I can find no mention of a pelvic girdle in female phallostethoids, but in the adult males the girdle is said to form part of the clasping organ (priapium). This is attached anteriorly to the tip of one or both forwardly-extended cleithra and is supported posteriorly by the two anterior ribs. The structure of the complicated priapium has been variously interpreted. Bailey (1936) tried to show a possible derivation from a pelvic girdle supported by a postcleithrum, as in *Polydactylus.* This interpretation seems incorrect because the phallostethoid structure which Bailey interpreted as a homologue of the postcleithrum is almost assuredly the modified rib of the third vertebra[3] and not part of the pectoral girdle.

Now, the adult male priapium consists of a number of specialized ossifications. Nevertheless, that part that is generally agreed to represent

[3] The third vertebra of females bears the usual, normally developed rib (Aurich, 1937: 265).

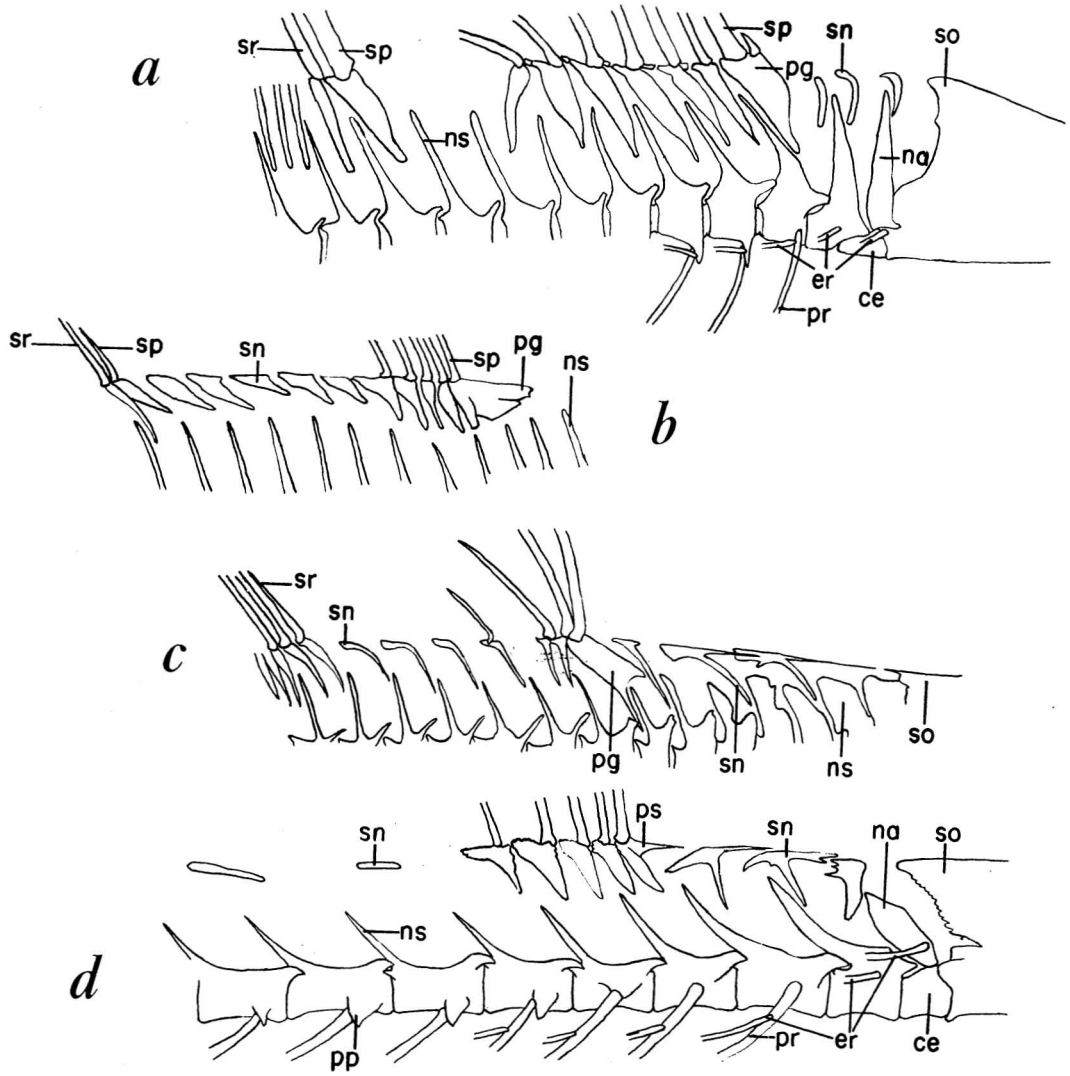

FIG. 3. Anterior dorsal fin supports and part of vertebral column of *a, Polydactylus sexfilis, b, Pranesus insularum, c, Mugil cephalus,* and *d, Sphyraena barracuda. ce,* Centrum; *er,* epipleural rib; *na,* neural arch; *ns,* neural spine; *pg,* pterygiophore; *pp,* parapophysis; *pr,* pleural rib; *sn,* supraneural; *so,* supraoccipital; *sp,* dorsal spine; *sr,* dorsal soft ray.

the pelvic girdle is supported by the modified ribs of the 3rd and 4th vertebra and does not extend forward to the cleithra.[4] The pelvic supports of the phallostethoid priapium would thus seem to show a considerably greater similarity to the rib supports of the pelvic girdle of atherinids than to either the polynemid or percoid condition.

[4] It is the specialized pulvinular structure of uncertain origin that articulates with the cleithra.

Other similarities between the phallostethoids and atherinids are the small, anteriorly placed spinous dorsal (when present), which has already been mentioned, the upwardly directed mouth, and the fact that both groups lay eggs with adhesive filaments (Villadolid and Manacop, 1934). There thus seems every reason to accept Myers' (1928) original placement of the phallostethoids next to the Atherinidae.

DISCUSSION AND CONCLUSIONS

The present author would agree with Myers (1935) and Hubbs (1944) that the Polynemidae, Sphyraenidae, Mugilidae, Atherinidae, and Phallostethoidei are more closely related to one another than to other fish groups. Nevertheless these five groups have diverged widely, and distinctive characters held in common by all of them are lacking. Apparently the best that can be done by way of defining the group as a whole is as follows:

Fishes that are basically percoid except in pelvic structure; pelvics never thoracic, either subabdominal with a spine and five soft rays, vestigial, or lacking; pelvic girdle never attached to the cleithral symphysis directly or by ligament. Spinous dorsal fin, if present, well separated from the soft dorsal.

Reasons have been given for believing that the pelvic morphology in these fishes is one that has never reached the percoid level of evolution. Whether or not this is so, a series of other structural features, e.g., the supramaxillary and the trisegmental dorsal ray supports in the Sphyraenidae indicate that they must have been derived from a very low level of percoid, if not of prepercoid, evolution. To state this conversely, the polynemids and sphyraenids cannot possibly have arisen from any advanced percoid groups. This being so, the whole series should stand before or at the bottom of the Perciformes in any teleostean classification.

Because of the great divergence among the groups under consideration, and because of the already tremendous size of the order Perciformes, it is perhaps most convenient to consider these fishes as a separate order Mugiliformes = Percesoces sensu Myers, 1935. The alternative is to consider the Mugiliformes as a suborder of the Perciformes. If this were done, it would seem necessary to include other groups such as the Scorpaeniformes as well, thus enlarging the Perciformes still further.

If the Mugiliformes is considered as an order, there is no particular objection to dividing it into three suborders in the way Myers proposed in 1935, namely Polynemoidei, Mugiloidei, and Phallostethoidei. Other ways of expressing the interrelationships might be equally good, but there seems no reason for merely substituting one equally good classification for another.

The following diagnosis attempts to express increasing levels of divergence from what is presumed to be the basal stock (peculiarities developed within groups are omitted here).

1a. Pelvic girdle supported by a postcleithral strut; vertebrae 24–26; eggs not adhesive.
  2a. Supraoccipital and frontal-parietal crests present. First dorsal spine over the 3rd vertebra; third and fourth upper pharyngeals separate; infraorbital canal complete; pectorals low or median ..... Polynemidae
  2b. No crests on top of skull.
    3a. Supramaxillary present; first dorsal spine over the 4th vertebra; third and fourth upper pharyngeals separate; infraorbital canal complete; pectorals on middle of sides ..... Sphyraenidae
    3b. No supramaxillary; first dorsal spine over the 7th vertebra; third and fourth upper pharyngeals fused; infraorbital canal interrupted; pectorals high on sides..... ..... Mugilidae
1b. Pelvic girdle not supported by postcleithral strut; vertebrae more than 26; eggs usually adhesive. Spinous dorsal, if present, placed well back on body; pectoral fins high on sides.
  4a. Pelvic fins present, with a spine and five soft rays; spinous dorsal present. Third and fourth upper pharyngeals fused; infraorbital canal interrupted ..... Atherinidae
  4b. Pelvic fins absent or rudimentary; spinous dorsal absent or reduced..... ..... Phallostethoidei

In whatever way the members of these groups are classified, certain aspects of interrelationship deserve reiteration. First, the Polynemidae and Sphyraenidae retain more generalized features than the others. Conversely, the Atherinidae, at least as represented by *Pranesus,* appears to be more generally divergent from the basal stock than the Polynemidae, Sphyraenidae, and Mugilidae. Finally, the phallostethoid families seem to have been derived from an atherinid-like ancestor, as Myers (1928) originally suggested.

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